The Condor 89:768–778

ATTENDANTS AT TREE SWALLOW NESTS. III. PARENTAL RESPONSES TO LIVE AND STUFFED-MODEL ATTENDANTS[1]

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Abstract. Attendants are common at Tree Swallow (*Tachycineta bicolor*) nests during the nestling period. Parent-attendant interactions were studied at a Tree Swallow nest box trail in New York. Attendants did not cooperate with parents (Lombardo 1986a) and were hypothesized to be individuals in search of potential future nest sites (Lombardo 1987). Therefore, they posed several potential threats to parental reproductive success.

Even though parents commonly encountered attendants at their nests, parent-attendant interactions were usually nonhostile. Parents were very unresponsive to model-attendants during the nestling period. Parents infrequently chased live attendants or attacked model-attendants presumably because the potential threats posed by attendants were rarely realized. Attendants were most active late in the breeding season when it was too late for attendants capable of breeding to breed successfully. Hatching year attendants had little to gain by behaving aggressively towards parents. This mutual restraint in conflict could be maintained by reciprocity (Lombardo 1985).

Key words: Tree Swallow; nesting behavior; aggression; mutual restraint.

INTRODUCTION

Attendants (i.e., conspecific individuals exclusive of the breeding pair) are common at Tree Swallow nests throughout the breeding season (e.g., see Kuerzi 1941, Tyler 1942, Sheppard 1977, Stutchbury 1984, Lombardo 1986a). Attendants include sexually mature individuals of both sexes, and late in the breeding season, recently fledged birds (Lombardo 1986a). Leffelaar and Robertson (1985) and Stutchbury and Robertson (1985) showed that sexually mature attendants at nests during egg laying, incubation, and the early nestling period are searching for exploitable breeding opportunities (e.g., nest usurpation). I showed that attendants were not helpers at the nest and had no demonstrable effect on parental reproductive success at my study site in New York (Lombardo 1986a). However, Robertson and Stutchbury (pers. comm.) observed a subadult female commit infanticide at their study site in Ontario. I have presented evidence that supports the hypothesis that hatching year attendants that are common late in the breeding season are searching for potential future nest sites (Lombardo 1987).

Given that Tree Swallow nest attendants are noncooperative and that several lines of evidence suggest that attendants are in search of present or future breeding opportunities, attendants and parents have a conflict of interest. Because parents are attempting to rear as many young to independence as possible with the minimum required effort, attendants present several potential threats to parental reproductive success. These threats are dependent upon the chronology of attendant behavior and include (1) intraspecific killing (Kuerzi 1941, Lombardo 1986b, Robertson et al. 1986), (2) nest usurpation (Kuerzi 1941, Stocek 1970, Leffelaar and Robertson 1985), (3) cuckoldry (but see Leffelaar and Robertson 1984), (4) mate loss (Kuerzi 1941, Stocek 1970, Leffelaar and Robertson 1985), (5) intraspecific brood parasitism (Lombardo, in press), (6) infanticide (Shelley 1934, Leffelaar and Robertson 1985), (7) the disruption of parental feeding schedules (Lombardo 1986a), (8) the transmission of disease and ectoparasites from attendants to young in the nest (Alexander 1974, Hoogland and Sherman 1976, Brown and Brown 1986), and (9) the attraction of diurnal avian predators to the nest by attendant activity.

In this paper, I examine the responses of parents to live and stuffed-model nest attendants at their nests during the nestling period. The results show that despite the conflict of interest between parents and attendants during the nestling period

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[1] Received 22 October 1986. Final acceptance 27 April 1987.

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(items 6 through 9 above), the interactions between them were generally nonaggressive.

METHODS

The study was conducted from 1980 to 1983 at a nest box trail located on the salt marshes of the John F. Kennedy Memorial Wildlife Refuge (JFKMWR) at Tobay Beach on the south shore of Long Island, New York. The study site has been described in detail elsewhere (Schaeffer 1972).

MARKING

Breeding females were captured on the nest on the first day of incubation (Kuerzi 1941, DeSteven 1980, Burtt and Tuttle 1983). Breeding males were usually captured and banded 1 to 2 days after eggs hatched. Some males were banded earlier when they were fortuitously captured in nest boxes during regular censuses. Males and attendants were usually captured at nest boxes using a radio-controlled trapping device (Lombardo and Kemly 1983). Birds were sexed by noting the presence of a well-developed brood patch in females or a cloacal protuberance in males. Prior to capture, attendants and breeders were identified by behavioral differences and breeding individuals in full adult breeding plumage (see below) were sexed using the criteria listed by Cohen (1984).

Each captured bird was banded with a U. S. Fish and Wildlife Service aluminum band and uniquely color-marked on its tail, wings, forehead, throat, or breast feathers using a marking pen or Testors Airplane Dope (Samuel 1976).

TREE SWALLOW COLOR MORPHS

The breeding population consisted of (1) subadult females: mostly yearling and some older females in brown plumage with varying amounts of iridescent feathering, (2) green females: most third year and all older females were in full iridescent plumage, and (3) green males: all males were in full iridescent plumage before their first winter (Dwight 1900, Cohen 1980, Hussell 1983). The iridescent plumage of swallows at my study site appeared more green-blue than blue-green. Forty-nine percent of breeding females were subadult females (Lombardo 1986c).

Throughout, "G-attendants" refers to attendants in full iridescent plumage and includes both males and females; "SAF-attendants" refers to female attendants in subadult female plumage; "HY-attendants" refers to attendants with a dusky-gray-brown plumage with no iridescent feathers (i.e., hatching year birds) and a faint chest band. On the wing, HY-attendants appeared smaller and less robust than SAF-attendants. I was not able to sex HY-attendants by gross examination. However, banding data showed that HY-attendants were of both sexes (Lombardo 1986a). The term "attendants" refers to the sum of G- + SAF- + HY-attendants.

BASIC OBSERVATION TECHNIQUES

Attendants were any swallows exclusive of the breeding pair that visited nests during the nestling period. Observations were concentrated during the nestling period because I never observed nest attendants before the nestling period during 137 hr of observations at 26 nests during 1980 and 1981. Because some attendants had previously bred in the same season (Lombardo 1986a), *nonbreeder,* the former designation for these individuals (Lombardo 1985), is inaccurate and has been abandoned.

From 1980 to 1983, 39 randomly chosen breeding pairs were observed for 60 min at least every third day from the hatching of their eggs to the fledging of their young. The order in which pairs were observed each day was determined by rolling a die. On average, four to six pairs were observed daily, usually between 06:00 and 14:00 EDT. A total of 488 hr of observations of 39 pairs were recorded during the nestling period ($\bar{x}$ = 12.5 hr/pair; range: 1–19 hr/pair). During observations I recorded the identity (e.g., parent or attendant) and the behavior of birds around the focal nest box. Another 28 pairs that fledged young were observed less frequently. I used both an 8 × 40 mm pair of binoculars and a 25×, 50 mm telescope to observe birds.

A parent-attendant *encounter* is defined as any time a parent, alone or with its mate, and one or more attendants were simultaneously present at, or within 3 m of, a nest box. A *chase* is defined as when one bird actively chased another, or displaced another from a perch. Encounters and chases are reported as $\bar{x} \pm$ SE/hr.

MODEL PRESENTATION EXPERIMENT

Models were presented to parents on day 12 of the nestling period (the day the first egg hatched = day 1) at each nest in 1983 in an effort to determine the effect of model plumage color and pa-

TABLE 1. Parental chases of live attendants during the nestling period.

Attendant type	Parent type[1]				Parent subtotals[2]		Total
	MGF	GF	MSAF	SAF	Male	Female	
Green	61[3]	33	36	16	97	49	146
Subadult female	20	15	9	10	29	25	54
Hatching year	35	24	13	5	48	29	77
Total	116	72	58	31	174	103	277

Parents did not chase all attendant types with equal frequency (Kruskall-Wallis, $\chi^2 = 36.95$, df = 2, $P < 0.001$). Chases of each attendant type were independent of parent sex ($\chi^2 = 2.75$, df = 1, $P > 0.25$), parent type ($\chi^2 = 8.21$, df = 6, $P > 0.10$), and parent color ($\chi^2 = 4.64$, df = 2, $P > 0.05$).

[1] MGF = male mated to a green female; GF = green female; MSAF = male mated to subadult female; SAF = subadult female. Hours of observations = 294 at the nests of green females and 194 at the nests of subadult females.

[2] Male = MGF + MSAF; Female = GF + SAF.

[3] Number of parental chases of attendants.

rental sex and plumage color on parental responses to model-attendants.

The two birds used as model-attendants were found dead (causes unknown, but see Lombardo 1986c) in nest boxes in May 1982 and were frozen until they were stuffed in February 1983.

The *G-model* was in full adult breeding plumage and represented all G-attendants. The *SAF-model* was in subadult female plumage and represented SAF-attendants and HY-attendants. Less than 25% of its dorsal feathers were iridescent (see Hussell 1983). The equality of parental responses to live SAF- and HY-attendants (see Results) justified the use of one model to represent all nongreen attendants.

The two models were presented simultaneously so that parents had a choice of which model to respond to first. The rationale for this method was the assumption that when given a choice parents would respond first to the model they perceive to be the greater threat to their reproductive success.

The models were mounted on the top of 1-m poles, and the poles were positioned 2 m apart and 1 m from the front of a nest box. Each model was equidistant from the nest box hole. The position of the SAF-model to the right or left of the nest box hole was determined by flipping a coin before each presentation.

I waited for the parents to go out of my sight before I positioned the models. The models were covered during positioning. When the parents returned I recorded the first model each responded to and the number of times each parent, (1) hovered over, (2) dove at, or (3) made contact with each model for 5 min. If parents did not return to their nest within 5 min of my positioning the models, I removed the models and rescheduled the experiment at that nest. Responses to models are reported as $\bar{x} \pm$ SE responses/5 min.

RESULTS

PARENTAL RESPONSES TO LIVE ATTENDANTS DURING THE NESTLING PERIOD

Parents encountered attendants 1,175 of the 1,669 (70.4%) times attendants were observed during 488 hr at 39 nests during the nestling period.

Parent-attendant interactions during encounters varied in intensity. During some encounters, parents appeared to ignore attendants and continued to visit their nests as if the attendants were not present. However, parents aggressively chased attendants from sight during 277 of 1,175 (23.6%) encounters (see Table 1).

Parental chases varied in intensity. During some chases parents simply intercepted an attendant in flight near their nest box and silently followed it until it flew away from the immediate area of the nest. However, during other encounters parents pushed perched attendants from the nest box and then closely chased them out of view while emitting alarm notes. Sometimes, parents displayed these disparate responses during a single observation period. The reason for changes in parental responses was often unclear because the switch from passive to aggressive response did not appear to be correlated with attendant identity or behavior.

Parental chases of attendants were relatively uncommon events (0.57 ± 0.05 chases/hr) given the frequency at which attendants were at their nests (3.14 ± 0.19 times/hr) and the rate that they were encountered by parents (2.39 ± 0.14 encounters/hr).

Parents chased all attendant types but did not chase all types with equal frequency (Table 1).

Parents chased G-attendants more often than either SAF-attendants or HY-attendants which they chased with equal frequency (Nonparametric Multiple Comparison, $P < 0.05$; Hollander and Wolfe 1973). This result was unchanged when the data were separately analyzed by breeding female color morph.

Breeding males chased attendants more than breeding females did (0.36 ± 0.03 chases/hr vs. 0.21 ± 0.03 chases/hr; Wilcoxon's Two Sample Test, $Z = 3.56$, $P < 0.001$; Table 1). This inequality was unaffected by breeding female color morph. Chases of each attendant type were independent of parent sex (Table 1). Even though females visited nests more frequently than males (7.80 ± 0.25 visits/hr, $n = 3{,}738$ vs. 6.60 ± 0.26 visits/hr, $n = 3{,}134$; Wilcoxon's Two Sample Test $Z = 3.39$, $P < 0.001$), there was no difference in the rate at which they encountered attendants (females, 1.14 ± 0.08 encounters/hr vs. males, 1.27 ± 0.08 encounters/hr; Wilcoxon's Two Sample Test $Z = 1.41$, $P = 0.59$). This is because when males were not delivering food to their young they were often perched on the box top or on a perch near the test.

Each class of attendant was chased at frequencies independent of parental type and parent color (Table 1). Encounter and chase rates were equal at the nests of green and subadult females suggesting that parent color had little influence on its frequency of chasing each type of attendant. G-attendants were chased the most (Table 1) regardless of who chased them.

There was a significant correlation between mean parental chases/hr and nestling age (Spearman's rho [ρs] = 0.609, $P = 0.01$, $n = 20$ days; Fig. 1). This result corresponded to the significant increase in mean attendant visits/hr with nestling age (Lombardo 1987). This result was unaffected by separately analyzing these data for either males and females or by breeding female color. Encounter rates also increased with nestling age (ρs = 0.932, $P < 0.001$, $n = 20$ days), suggesting that (1) the increased frequency of encounters was caused by the increase in attendant abundance with nestling age and (2) parental aggression toward attendants matched the frequency of their encounters with them.

The correlation between attendant abundance with nestling age was an artifact of the increase in attendants at the study site with calendar date (Lombardo 1987). Figure 2 shows the relationship between attendant visitation, parental encounter, and parental chase rates. The nestling period is divided into six blocks of 10 days each beginning on 31 May. When attendants increased in abundance so did parental encounters and chases, but after 19 June, attendant visitation rates outstripped encounter rates (Fig. 2). The rate that each type of attendant was chased followed the same pattern, an increase to a peak during a 10-day block which was followed by a precipitous decline (see Fig. 3). The peaks in parental chase rates of each type of attendant occurred at different times and matched the peaks in visitation rates for each type of attendant (Fig. 3).

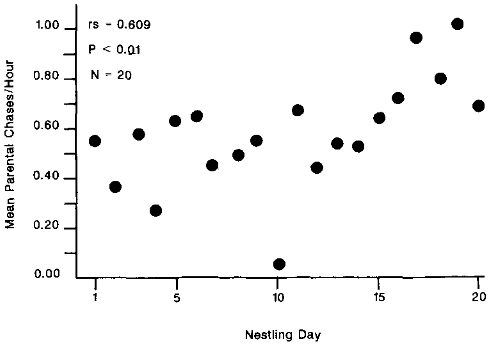

FIGURE 1. Mean parental chases/hr vs. nestling age.

ATTENDANT RESPONSES TO PARENTS DURING THE NESTLING PERIOD

All three types of attendants chased parents (Table 2). Attendants sometimes forcibly displaced parents from perches on the nest box by landing next to the parent and then pushing the parent. Attendants often dove sharply at parents perched at the nest box hole while parents prepared to enter to feed their young. The attendants landed on the parents' shoulders and pushed the parents from their footholds. Parents would frequently hover at the nest box hole until the attendant left its newly won perch, but sometimes they chased the attendant away.

Attendants chased parents in proportion to attendant abundance, so that parents were chased more frequently by G-attendants than any others (Table 2).

Attendants chased males and females in proportion to the rate at which they encountered parents of each sex ($\chi^2 = 2.06$, df = 1, $P > 0.10$).

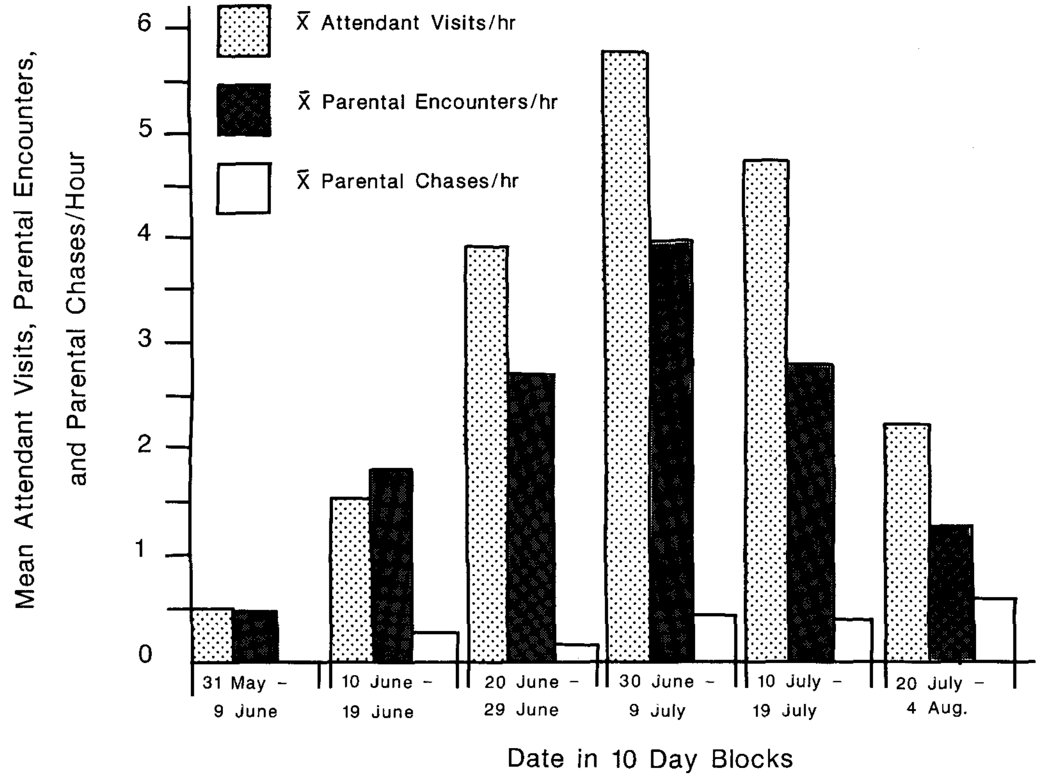

FIGURE 2. Mean attendant visititation, parental encounter, and parental chase rates vs. date.

Each type of attendant chased parents independently of breeding female color ($\chi^2 = 0.024$, df = 2, $P > 0.75$), parental sex ($\chi^2 = 0.139$, df = 2, $P > 0.90$), or parental color morph ($\chi^2 = 2.09$, df = 2, $P > 0.25$).

There was a significant correlation between mean attendant chases/hr and nestling age ($\rho s = 0.591$, $P < 0.01$, $n = 20$; Fig. 4). This corresponded to the increase in attendant visitation (Lombardo 1987) and encounter rates with nestling age (see above) and suggests that attendant aggression towards parents matched the frequency of their encounters with them.

Figure 5 shows the relationship between mean attendant visitation, parental encounter, and attendant chase rates when considered by date. Note that although mean attendant chases/hr significantly increased with date ($\rho s = 0.886$, $0.10 >$

TABLE 2. Attendant chases of parents during the nestling period.

Attendant type	Parent type[1]				Parent subtotals[2]		Total
	MGF	GF	MSAF	SAF	Male	Female	
Green	27[3]	14	9	10	36	24	60
Subadult female	7	5	3	3	10	8	18
Hatching year	7	8	6	1	14	9	23
Unknown identity	4	3	0	1	4	4	8
Total	45	30	18	15	64	54	109

Each attendant type did not chase parents equally (Kolmogorov-Smirnov, D = 0.261, $n = 109$, $P < 0.001$). Each attendant type chased parents in proportion to its attendance ($\chi^2 = 0.986$, df = 2, $P > 0.50$).

[1] MGF = male mated to a green female; GF = green female; MSAF = male mated to subadult female; SAF = subadult female. Hours of observations = 294 at the nests of green females and 194 at the nests of subadult females.

[2] Male = MGF + MSAF; Female = GF + SAF.

[3] Number of attendant chases of parents.

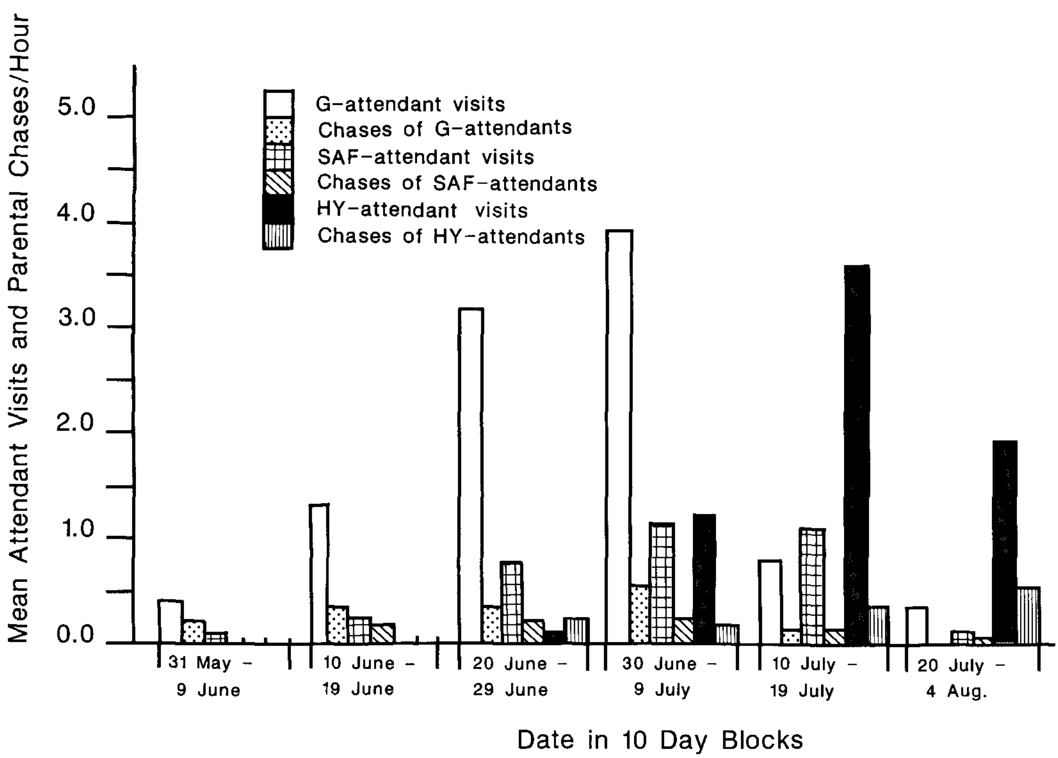

FIGURE 3. Mean attendant visitation and parental chase rates by type of attendant vs. date.

$P > 0.05$, $n = 6$; Fig. 5), 36.7% (40/109) chases occurred between 30 June and 9 July when attendants were most common (Fig. 5).

Attendants also chased young as they fledged. Five nestlings that I saw fledge naturally, and nine of 13 nestlings that I hand fledged when they were 22 days old were hostilely chased from view by attendants. Parents did not pursue their young or the attendants chasing them when they were present during attendant chases of fledglings (Lombardo 1987).

PARENTAL RESPONSES TO MODEL-ATTENDANTS

Parents were unresponsive to the model-attendants during the nestling period (Table 3). Parents responded to the models in 10 of 18 (56%) trials. At eight nests only one parent responded to the models (males, $n = 3$; females, $n = 5$). At these eight nests, parents responded to the SAF-model first. Males directed four of five, and females five of seven initial responses to the SAF-model. Among pairs with green females, eight of nine (89%) of initial responses were to the SAF-model. Within pairs with subadult females, only one of three initial responses was at the SAF-model.

The mean parental response rate to the models during the nestling period was 1.44 ± 0.44 ($n = 24$). The 24 responses to the models were not evenly distributed over all nests; six responses

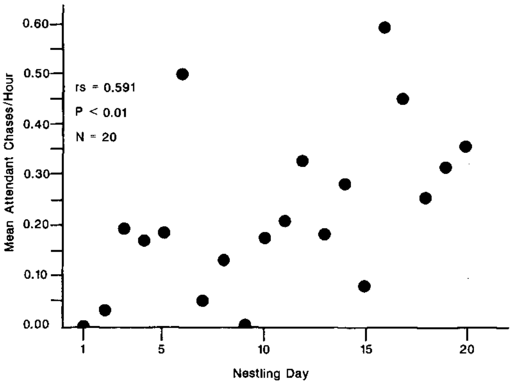

FIGURE 4. Mean attendant chases/hr vs. nestling age.

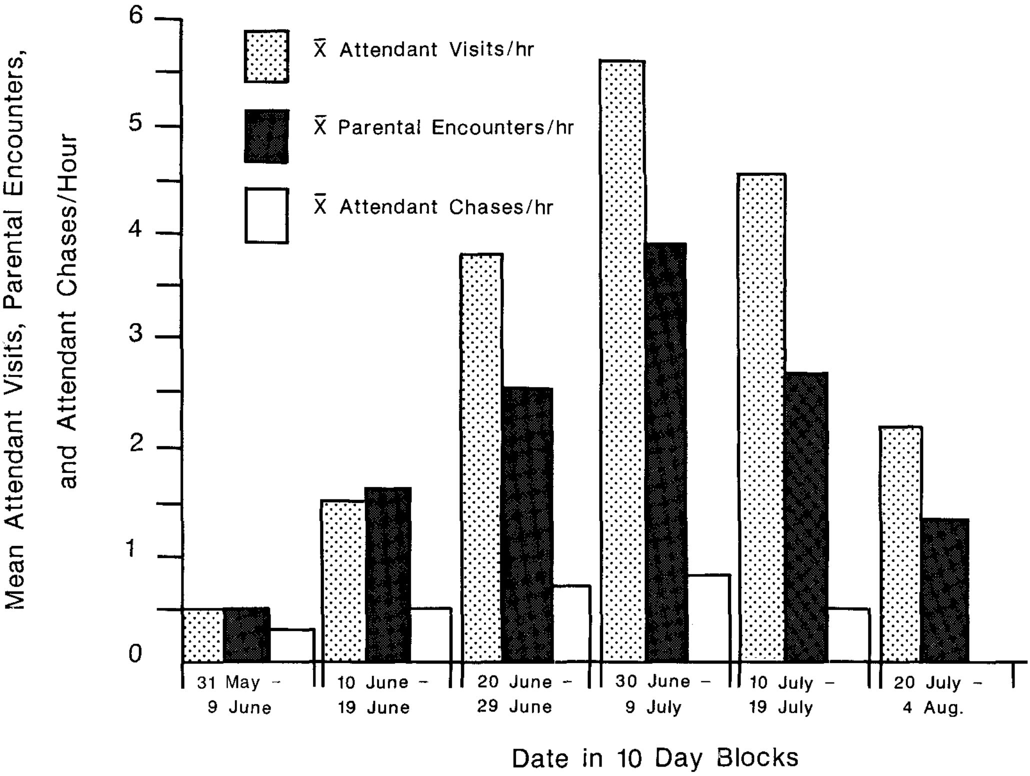

FIGURE 5. Mean attendant visitation, parental encounter, and attendant chase rates vs. date.

(25%) were performed by one male mated to a subadult female. This male accounted for six of the eight (75%) responses by pairs with subadult females. Likewise, one breeding green female was responsible for three of 11 (27%) female responses and 13% of all parental responses. Only four of 24 (17%) responses were contact responses. These four were performed by a male mated to a subadult female that aggressively contacted the SAF-model three times and a green female that contacted the G-model once.

Parental responses to each model type were independent of breeding female color, parental color, and parental sex (Table 3). However, parents responded more to the SAF-model than expected ($\chi^2 = 3.85$, df = 1, $P < 0.05$) under the null hypothesis of equality of responses to each model.

DISCUSSION

Given the hypothesis that attendants are individuals in search of potential future nest sites (Lombardo 1987), the apparent lack of attendant cooperation in parental breeding (Lombardo 1986a) was not surprising. However, given the conflicts of interest between parents and attendants at active nests, there was greater restraint in parent-attendant interactions than expected; 789 of 1,175 (67.1%) interactions were nonaggressive.

Although attendants presented several potential threats to parental reproductive success during the nestling period, these threats were rarely manifested. Infanticide is the most direct threat to parental reproductive success. Only one nestling from 76 broods was found dead with the peck wounds on the head that are associated with avian infanticide (e.g., see Shelley 1934, Stacey and Edwards 1983, Crook and Shields 1985, Leffelaar and Robertson 1985, Romagnano et al. 1986).

Attendants disrupted parents while they were feeding their young by (1) harassing parents around the nest, (2) chasing parents, and (3) attempting to steal food from parents and nestlings (Lombardo 1986a). However, attendants infre-

TABLE 3. Parental responses to model-attendants during the nestling period.

	Parent type[1]				Parent subtotals[2]		
Model	MGF	GF	MSAF	SAF	Male	Female	Total
Green	1[3]	3	3	1	4	4	8
Subadult female	7	7	3	1	10	8	18
Total	8	10	6	2	14	12	26

Parental responses to each model type were independent of breeding female color ($\chi^2 = 2.01$, df = 1, $P > 0.01$), parent color (Fisher Exact Test, $P = 0.529$), and parent sex ($\chi^2 = 0.0609$, df = 1, $P > 0.75$).

[1] MGF = male mated to a green female; GF = green female; MSAF = male mated to subadult female; SAF = subadult female. There were 12 trials at the nests of green females and six trials at the nests of subadult females.

[2] Male = MGF + MSAF; Female = GF + SAF.

[3] Number of parental responses to model-attendants.

quently chased parents; 109 of 1,175 (9.3%) encounters resulted in chases. Attendant attempts to steal food from parents and nestlings could potentially have severe consequences on parental reproductive success if the weather is cold and wet and nestlings are small (e.g., see Bryant 1975, 1978; Quinney et al. 1986; Lombardo 1986a) because bad weather lowers insect abundance (Williams 1961, Taylor 1963) and increases the chances of nestling hypothermia in small poikilothermic nestlings (Dunn 1979). However, there was no evidence that attendant competition for food was a source of nestling mortality during the course of this study. In fact, attendant attempts to steal food from either parents or nestlings were very rare (Lombardo 1986a).

Alexander (1974) hypothesized that the epidemic spread of diseases and parasites was a cost of group living. Hoogland and Sherman (1976) and Brown and Brown (1986) showed a positive correlation between colony size and ectoparasite infestation in the Bank Swallow (*Riparia riparia*) and Cliff Swallow (*Hirundo pyrrhonota*), respectively. During 1982 and 1983, several broods were infested with mites. Mite infestations can have a significant effect on reproductive success (e.g., see Moss and Camin 1970). Attendants, because they visited several nests, could have transmitted mites from infected to uninfected nests. However, mite infestations did not appear to spread throughout the study site after they were discovered in one nest. Nests adjacent to heavily infested nests did not become infested. These observations suggest that the phoretic spread of ectoparasites from nest to nest by attendants was not an important threat to parental reproductive success at my study site. In fact, a heavy mite infestation appeared to contribute to nestling mortality in only one of 76 (1.3%) broods produced from 1980 to 1983. In 1982, all five nestlings of one brood died during a heavy mite infestation. Each nestling lost an average of 20.8% of its body weight between nestling day 12 and their deaths on nestling days 15 and 16.

Alexander (1974) suggested that an increased vulnerability to predation relative to that of a solitary existence is a potential cost of group living. Although Tree Swallows are not colonial (Sheppard 1977, Muldal et al. 1985), they will nest in aggregations (Whittle 1926, Kuerzi 1941, Sheppard 1977, this study) if suitable nest sites are located near one another. Because nests with nestlings attracted the most attendants (Lombardo 1987), there was a great deal of activity around these nests. This type of activity could alert diurnal avian predators to the location of active nests, and therefore represent a threat to parental reproductive success. However, it is unlikely that this potential threat is ever realized because I saw an accipiter (species unidentified) attack a group of attendants examining a nest just once during 488 hr of observations. The attack was unsuccessful. Thus, the potential threat to parental reproductive success due to predation attracted by attendant activity appears to be small. In fact, parental reproductive success actually may be enhanced by attendant activity during an attack by a predator because attendants mobbed potential predators (Lombardo 1986a).

I believe that parents were usually nonaggressive towards both live and stuffed model attendants because attendants represented little threat to parental reproductive success during the nestling period. In contrast, parents were very aggressive toward stuffed model-attendants during the egg-laying and incubation periods (Lombardo 1984) when there was a greater chance of the threats (e.g., mortality or injury from fighting, nest usurpation, mate loss) posed by attendants being realized (e.g., see Kuerzi 1941, Stocek 1970, Leffelaar and Robertson 1985, Lombardo 1986b, Robertson et al. 1986).

However, it is likely that the lack of parental aggression during the nestling period may have also been influenced by the potentially greater costs of aggression during the nestling period relative to egg laying and incubation. Bryant and Westerterp (1980) have shown that the highest daily rates of energy expenditure were recorded during the nestling period in the ecologically similar Common House-Martin (*Delichon urbica*). Thus, parents would waste valuable time and energy chasing fairly nonaggressive attendants during the nestling period when that energy could be more profitably devoted to rearing young.

When parents were hostile towards live attendants, they chased G-attendants the most. However, the greater hostility toward G-attendants was an artifact of the greater abundance of G-attendants (Lombardo 1986a). This is supported by the observation that the chase rates of each type of attendant followed peaks of attendant abundance when calendar date was considered (Fig. 3). This result implies that parents reacted to attendants at their nests and not the type of attendant. However, male aggression decreased and female aggression increased as the season progressed. This pattern coincides with the changes in abundance of green and brown colored SAF- and HY-attendants (Lombardo 1987), respectively, and implies that parents were sensitive to the attendant type that was most likely to be a direct competitor with them. For example, males were most aggressive toward attendants that were most likely to be other males (i.e., G-attendants). However, these results can also be partially explained by the observations that (1) males fed nestlings less than females and (2) only females brooded young during the first 5 days of the nestling period (Lombardo 1984). Thus, males have more time and energy relative to females to devote to chasing attendants. As the nestling period progressed, males and females contributed equal proportions of feeding visits (Lombardo 1984) freeing females to chase attendants.

Parents responded more to the SAF-model than the G-model and parents in green female pairs directed a significant proportion of their initial responses at the SAF-model. These results suggest that parents perceived the SAF-model as a greater threat to their reproductive success than the G-model. The literature is replete with observations of aggressive encounters between mated females and late arriving subadult females (e.g., see Shelley 1934, Bagg and Eliot 1937, Kuerzi 1941, Tyler 1942, Stocek 1970, Sheppard 1977, Stutchbury 1984, Leffelaar and Robertson 1985). The general impression of these observers was that the subadult females initiated this aggression in their attempts to drive the resident female from her mate and nest.

Attendants chased parents and fledglings, but this behavior is expected if attendants were searching for potential future nest sites (Lombardo 1987) and viewed parents and fledglings as competitors. These results, in conjunction with the observation that attendants also chased one another, support the hypothesis that attendants were searching for potential future nest sites and were aggressive toward individuals that were potential competitors in their endeavor. However, less than 10% (109/1,175) of attendant-parent encounters resulted in attendants behaving aggressively towards parents.

Why weren't attendants *more* hostile in their interactions with parents? Attendants, especially HY-attendants, would have gained little by being aggressive during the nestling period. The greatest period of attendant activity occurred after the latest date of clutch initiation that resulted in fledged young (Lombardo 1987). Thus, when sexually mature attendants were most active it was too late for them to initiate breeding and successfully rear young to fledging. From 21 June until 9 July, 55 of 754 (7.3%) encounters resulted in attendants chasing parents. The latest date of the successful initiation of breeding was 25 June.

HY-attendants were incapable of breeding, and thus had more to gain by learning the location and characteristics of future potential nest sites (Lombardo 1987) than by attempting to harm the reproductive success of parents (Lombardo 1985). After 9 July nearly all attendants were HY-attendants (Lombardo 1987). From 9 July until the end of the breeding season, attendants did not chase parents in 155 of 190 encounters with them (81.6%).

Another experiment showed that the mutual restraint in conflict demonstrated by parent and attendant Tree Swallows during the nestling period could be maintained by reciprocity (Lombardo 1985) as described by the TIT FOR TAT model (Axelrod and Hamilton 1981).

ACKNOWLEDGMENTS

I thank H. W. Power, E. Litovich, M. Fitch, G. Shugart, T. R. McGuire, E. W. Stiles, B. G. Murray, Jr., J. Burger, and R. R. Cohen for their help throughout the course of my study. L. C. Romagnano, E. D. Kennedy, and especially W. M. Shields provided cogent comments on the manuscript. The Town of Oyster Bay, New York kindly allowed me to use the Kennedy Refuge as a study site. Financial support was provided by a BRSG Grant to H. W. Power from Rutgers University and from grants from the F. M. Chapman Fund, the Northeastern Bird Banding Association, Sigma Xi, the J. Leathman Fund of the Zoology Department and the Ecology Graduate Program of Rutgers University.

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